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Manipulating Beaver (*Castor canadensis*) Feeding Responses to Invasive Tamarisk (*Tamarix* spp.)

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Abstract To evaluate methods for promoting consumption of tamarisk plants by beavers (*Castor canadensis*), we determined the feeding responses by captive beavers to diets that contained tannins and sodium chloride (hereafter referred to as tamarisk diet). In two-choice tests, beavers consumed equivalent quantities of tamarisk diet and control diet. Treatment with polyethylene glycol and fructose did not increase beaver preferences for the tamarisk diet. When offered the choice of control diet and casein hydrolysate-treated control diet, beavers strongly avoided the latter, showing feeding deterring activity of casein hydrolysate. However, when tamarisk diet was the alternative to the deterrent treatment, beavers consumed similar quantities of the two diets. Finally, beaver foraging preferences for actual plant cuttings were assessed. Casein hydrolysate application to cuttings of black poplar (*Populus nigra*) and Scouler's willow (*Salix scouleriana*) reduced browsing of these highly preferred species and promoted a marked increase in browsing of tamarisk (*Tamarix ramosissima*). These results suggest that casein hydrolysate treatment of desirable riparian plant species such as *Salix* and *Populus* may promote beaver foraging of invasive tamarisk.

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Introduction

In a classic example of ecosystem engineering, beavers (*Castor canadensis*) significantly impact riparian ecosystems. Models suggest that dam-induced flooding has lasting effects on the vegetative structure of riparian areas (Sturtevant 1998). Removal of dominant tree and shrub species for food and structure-building further alters plant species composition of riparian communities (Martell et al. 2006). Damage to agriculture, dwellings, and roads caused by dam building and tree cutting is widespread in North America. In just one example, beaver activity was identified as the sole source of vegetation loss at the Tres Rios demonstration wetlands near Phoenix, AZ, USA, severely hampering efforts to recreate historical wetlands (Nolte et al. 2003). In some areas, desirable plants such as poplar (*Populus* spp.) and willow (*Salix* spp.) were completely removed by cutting, girdling, and/or burrowing by resident beavers.

Riparian areas are also subject to displacement of native plant species by invasive plants such as tamarisk (*Tamarix* spp.). Tamarisk, a Eurasian shrub/tree, has fundamentally altered riparian community composition and ecosystem properties by out-competing native riparian vegetation in riparian areas (Busch and Smith 1995). Tamarisk invasions alter litter leaf quality (Bailey et al. 2001), reduce algal production via shading (Kennedy and Hobbie 2004), and disrupt riparian ecosystem function (Busch and Smith 1995). Beaver activity may aggravate tamarisk invasions. In eastern Montana, tamarisk growth rate substantially increased where beavers had reduced the canopy of native plant species (Lesica and Miles 2004). Whereas beaver-caused mortality to poplar was extensive in this study (as high as 80% at some sites), beaver use of tamarisk was not observed at any of the ten study sites.

Tamarisk is considered undesirable forage because of low nutritive content and the presence of numerous poly-phenolic compounds, including flavonoids, hydrolyzable and condensed tannins (Sharma and Parmar 1998). In addition, deciduous leaves of *Tamarix* species have elevated levels of sodium and salts of other alkali and alkaline earth metals present on the surface of the leaves in specialized glands (Kleinkopf and Wallace 1974). Sodium is one of many micronutrients required by herbivores. However, these nutrients are avoided when they are in excess (Villalba and Provenza 1996).

Mammalian species limit tannin intake when they lack the salivary proteins to bind tannins and render them innocuous (Hagerman and Robbins 1993). Beavers produce a single protein that binds to linear condensed tannins found in plants common to their diet (such as willow and poplar species) but not to branched condensed tannins (quebracho) or hydrolyzable tannins (Hagerman and Robbins 1993). Despite the presence of polyphenolics and highly elevated sodium chloride (NaCl) concentrations, a few mammalian herbivores are known to consume tamarisk. For example, goats can be enticed to consume tamarisk plants, and thus may represent a component of an integrated management plan for tamarisk removal (Richards and Whitesides 2006). Valley pocket gophers (*Thomomys bottae*) have been observed to forage tamarisk roots (Manning et al. 1996), and there have been anecdotal reports of beaver feeding on localized populations of tamarisk (Bergman, personal communication).

Diet preferences are strongly impacted by the post-ingestive consequences of food consumption (Provenza 1995). Phytochemicals that act on the sensory and gut systems of herbivores influence what plants or plant parts are eaten, when they are eaten, and how they are eaten. The poor palatability of tamarisk may be related, in part, to the nutritional status of the animal, hedonic qualities of the plant, and postingestive consequences that result from tannin binding of beneficial proteins. Supplements, analgesics, and masking agents can be used to minimize the antifeedant effects of tamarisk phytochemicals. For example, in humans, salty taste is reduced by addition of equimolar sucrose to salt solutions (Bartoshuk 1975). Astringency and postingestive effects of tannins can be reduced with polyethylene glycol (PEG), which irreversibly binds tannins and promotes intake of high tannin-containing plants by goats (Titus et al. 2001) and lambs (Titus et al. 2000). Accordingly, by alleviating or masking the negative attributes of tamarisk, one could promote its consumption by beavers.

Diet selection is influenced by the availability of food alternatives. The mere presence of multiple sources of the same food can drastically impact what foods are consumed and how much (Tordoff and Bachmanov 2003). Availability and nutritive quality of alternative foods influence the persistence of learned preferences (Kimball et al. 2002). Conversely, the limiting of foraging alternatives can be used to promote consumption of targeted food sources. In managed ecosystems, availability of desirable resources can be limited by exclusion (e.g., fences) and/or deterrent application (Nolte 1999). Thus, the application of an herbivore deterrent to desirable forage plants such as willow and poplar could promote tamarisk consumption by beavers.

A series of experiments was conducted with captive beavers to assess the feasibility of promoting consumption of tamarisk by altering its palatability with topical application of PEG and sugar and/or treatment of native plants with a deterrent.

Methods and Materials

Subjects Beavers were trapped in watersheds located near Olympia, WA, USA, and maintained in individual 3×5 m pens. The 1.5-m tall pen walls were clad with sheet metal. Each pen contained a 1,000-l corrugated steel water tank and insulated den box. Fresh water and a pelleted ration (Lab Diet 5012; PMI Nutrition International, Richmond, IN, USA) were provided in stainless steel food bowls. Diet enrichment consisted of apples, carrots, and dried corn on the cob. Animal procedures were approved by the National Wildlife Research Center (NWRC) Institutional Animal Care and Use Committee. All experiments were conducted during the period of June–August 2007.

Test diets Test and control diets were prepared commercially by Dyets (Bethlehem, PA, USA) with Purina Prolab RMH-1000, a commercial rat/mouse/hamster diet made from wheat, corn, and bone meal (as well as many other minor constituents, vitamins, and minerals). Maltodextrin and gum Arabic were added to both diets to confer integrity to the pellets in the wet environment anticipated in the pens. The control pellet was prepared with 15% cellulose (Dyets) (Table 1). All test pellets (approximately 45×12 mm diameter) were offered to the captive subjects in stainless steel food bowls.

Tamarisk leaves are high in tannins (Bailey et al. 2001), and sodium concentrations can far exceed 10% in plants growing in highly saline conditions (Kleinkopf and Wallace 1974). Leaf litter tannin content from *T. ramosissima* collected in Nevada, USA, was greater than 10% (Kennedy and Hobbie 2004). Thus, the tamarisk diet pellets contained

Table 1 Pelleted test diets used in two-choice tests with beavers

Ingredient	Control diet (%)	Tamarisk diet (%)
Purina RMH-1000	81	81
Cellulose	15	–
Sodium chloride (NaCl)	–	5
Quebracho tannin	–	10
Maltodextrin	2	2
Gum Arabic	2	2

10% quebracho tannin (Tannin, Peabody, MA, USA) and 5% NaCl (Aldrich Chemical, Milwaukee, WI, USA). Quebracho tannin was used in the formulation of the test diet for this study because beavers are physiologically incapable of binding branched condensed tannins with salivary proteins (Hagerman and Robbins 1993).

Plant cuttings Cuttings of black poplar (*Populus nigra*) and Scouler's willow (*Salix scouleriana*) were obtained locally near the Olympia, WA, USA, pen facilities. Tamarisk (*Tamarix ramosissima*) cuttings were collected from an invasive population located on the Saddle Mountain National Wildlife Refuge in Central Washington (USA). One meter cuttings were made from lateral branches such that the diameter at the base of the branch did not exceed 10 mm.

Cuttings were offered to captive beavers by placing them in specially constructed racks attached to the sides of each test pen. Each rack consisted of two galvanized fence top-rail tubes (5 cm diameter). The base rail was mounted 20 cm from the floor of the pen, and the upper rail 80 cm above the base rail. Twelve holes were drilled in both rails at identical locations such that the holes were spaced every 40 cm. Short lengths (7 cm) of 20 mm conduit were tack welded in the holes. One end of each cutting was placed into the conduit in the lower rail and threaded through the conduit in the upper rail. Wood dowels (15 mm diameter) were wedged into the conduit of the top rails to hold the cuttings securely in place.

Treatments Polyethylene glycol 3350 (VWR International, West Chester, PA, USA), fructose (Aldrich Chemical), and casein hydrolysate (HCA-411, American Casein, Burlington, NJ, USA) were used to treat pellets in multiple experiments. Pellets were soaked briefly in a 1.0% (*v*/*v*) solution of a latex sticker (Tactic®; Loveland Industries, Greeley, CO, USA), drained of excess sticker solution, and dusted with either casein hydrolysate (deterrent treatment) or 1:1 PEG/fructose (tamarisk treatment) at an application rate of 120 g treatment per kg pellet. Treated pellets were allowed to dry before offering to the test subjects. Plant cuttings were treated by spraying the leaves with the sticker solution and dusting with casein hydrolysate powder by hand.

Bioassay procedures Acclimation to the bioassay procedures was achieved by offering all subjects the training diet (Purina 5012 pellets) in single-choice tests commencing at 0800 hours daily. At the end of the 24-hr test period, test diets were removed and weighed to determine intake by difference and replacement made with fresh diets. Ten subjects (of 15 initially captured) that successfully acclimated to captive conditions and readily consumed the training diet for at least four consecutive days were retained for experiments 1–4. Two additional subjects were subsequently added for experiment 5.

Experiments 1–4 were each conducted for four consecutive days with position of diets (right, left) randomly assigned and alternated daily. Water was provided *ad libitum.* During intermission periods between experiments, subjects were provided *ad libitum* access to the basal diet (Lab Diets 5012) supplemented with apple, carrot, and/or dried corn. Experiments were conducted sequentially with the same test subjects.

In experiment 1, all subjects were offered the control (cellulose) and tamarisk (tannin and NaCl) diets in separate containers, whereas all subjects in experiment 2 were offered control and treated tamarisk (PEG and fructose treatment) diets in a similar two-choice test (Table 2). Daily intake (24-hr) of each diet was recorded, and preference scores were calculated to describe the proportion of tamarisk diet consumed in the two-choice tests (tamarisk diet intake divided by total intake).

All subjects in experiment 3 were offered control and deterrent-treated control (casein hydrolysate) diets while experiment 4 consisted of tamarisk (untreated) and deterrent-treated control (casein hydrolysate) diets in two-choice tests (Table 2). Preference scores were calculated from the intake data to describe the proportion of deterrent-treated control diet consumed. Mean tamarisk diet intake (g) in experiments 1, 2, and 4 was also calculated for graphical evaluation.

In experiment 5, subjects were assigned to one of two treatment groups such that training diet intake was similar between treatment groups. Two naïve subjects were included in experiment 5 (one per treatment group) for a total of 12 beavers. Subjects in the control group were

Table 2 Test diets and treatments offered to captive beavers in two-choice experiments

Experiment	Diet A	Diet B
1	Tamarisk diet	Control diet
2	PEG/fructose-treated tamarisk diet	Control diet
3	Deterrent-treated control diet	Control diet
4	Deterrent-treated control diet	Tamarisk diet

PEG: polyethylene glycol, *deterrent*: casein hydrolysate offered four cuttings each of black poplar, Scouler's willow, and tamarisk. The 12 cuttings were randomly placed in the 12 rack locations. Subjects in the treatment group were similarly offered cuttings of the three plant species except that the black poplar and Scouler's willow cuttings were treated with casein hydrolysate. Consumption of plant cuttings was scored according to the following ordinal scale: 1, no evidence of browse; 2, sampled; 3, moderate browse; 4, completely browsed. Plant cuttings were offered for 24 hr on four consecutive days. Cuttings were replaced at the end of each 24-hr period regardless of browse activity, and new random positions were assigned daily.

Statistical analyses For each of the two-choice tests, preference scores were rank transformed within subjects so that day and diet position (right or left position of the diet referred as the proportion) were analyzed as fixed effects by analysis of variance (ANOVA). Mean preference scores for each subject were compared to values of 0.5 (indifference) for each experiment by *t*-test according to the procedures described by Willink (2005) for skewed data.

Browse scores from experiment 5 were subjected to a three-way ANOVA with treatment (control or deterrent treatment), species (willow, poplar, or tamarisk), and day considered fixed effects. Multiple comparisons of least-square means were made by controlling false discovery rate (Benjamini and Hochberg 1995). All statistical analyses were performed with SAS (Cary, NC, USA).

Results

ANOVA results from all two-choice tests indicated that neither test day nor diet position impacted diet preferences. Therefore, mean preference scores were examined to determine preferences for the test diets in experiments 1–4.

In experiment 1, the mean proportion of tamarisk diet consumed by the ten beavers was 0.46, indicating that tamarisk diet intake did not significantly differ from the control (P=0.38; Fig. 1). Treatment of the tamarisk diet with fructose and PEG did not increase the proportion of tamarisk diet consumed in experiment 2. The proportion (relative to the control diet) of treated tamarisk diet consumed was 0.39 (P=0.21; Fig. 1).

Avoidance of casein hydrolysate was demonstrated in experiment 3. The proportion (relative to the untreated control alternative) of casein hydrolysate-treated control diet was 0.024, which was significantly less than 0.5 (P< 0.001; Fig. 1). However, when the alternative food choice was tamarisk diet in experiment 4, the proportion of deterrent-treated diet consumption increased to 0.44, indicating that tamarisk diet intake did not significantly differ from the casein hydrolysate diet (P=0.19; Fig. 1). The tamarisk diet intake data from experiments 1, 2, and 4 suggest a maximum intake that could be tolerated in a 24-hr feeding period, regardless of treatment or the alternative food choice (Fig. 2).

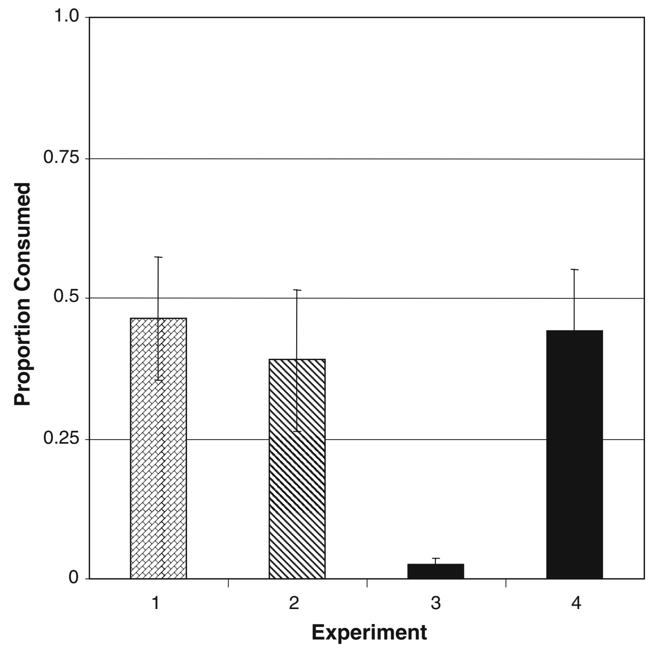

Fig. 1 Preference scores (mean+SE; N=10) for experiments 1–4 describing the proportion of test diet consumed (*crosshatched bars* untreated tamarisk diet, *diagonally hatched bars* sugar/PEG-treated tamarisk diet, *black bars* deterrent-treated control diet) in two-choice tests. The alternative diet for experiments 1–3 was untreated control. The alternative for experiment 4 was untreated tamarisk diet. A preference score of 0.5 indicates indifference. Results of *t*-tests indicated that only the casein hydrolysate preference score in experiment 3 was significantly less than 0.5 (P<0.001)

ANOVA results from experiment 5 demonstrated that browse score (i.e., preference for plant cuttings) was a function of test day (P=0.018), plant species (P<0.0001), and the species×treatment interaction (P=0.001). Browse scores were lower on day 4 of the test vs. days 1 or 3. Among the control group, foraging preference for the plants followed the order: willow>poplar>tamarisk (Fig. 3). However, deterrent treatment of willow and poplar promoted increased browsing of tamarisk and resulted in no significant preferences among the three species (Fig. 3).

Discussion

Herbivore preferences for various plant species are a function of maximizing nutritional benefits while at the same time limiting intake of plant secondary metabolites. For example, beavers strongly preferred aspen (*Populus tremuloides*) over red maple (*Acer rubrum*) in cafeteria tests despite having similar energy, protein, and fiber values (Doucet and Fryxell 1993). Differences in the palatability

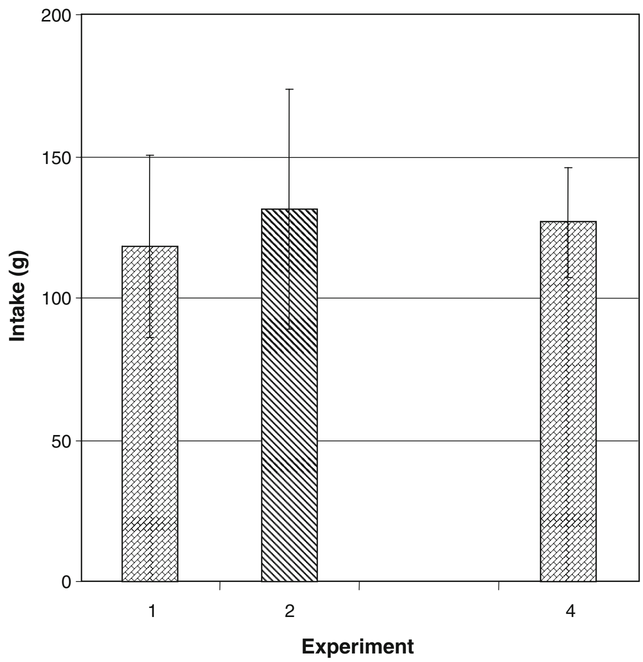

Fig. 2 Tamarisk diet intake (g) from experiments 1, 2, and 4 (mean+SE; N=10). The alternative diet for experiments 1 and 2 was untreated control diet. The alternative diet in experiment 4 was deterrent (casein hydrolysate)-treated control diet (*crosshatched bars* untreated tamarisk diet, *diagonally hatched bars* sugar/PEG-treated tamarisk diet)

of these species were a consequence of phenolic content, not absolute nutritional quality (Muller-Schwarze et al. 1994). Tamarisk can contribute to the nutritional needs of herbivores capable of tolerating the phenolics and NaCl present in the foliage. On a dry matter basis, tamarisk foliage contains approximately 13 kJ/g digestible energy, 21% crude protein, and 16% crude fiber (Kimball, unpublished data).

Tamarisk diet constituted one-half of the total consumption by beavers in experiment 1. Treatment with fructose (to suppress salt flavor) and PEG (to bind tannins) did not promote greater consumption of tamarisk diet in experiment 2. The lack of day effect in these experiments indicates that tamarisk diet intake limitation was not a function of conditioned aversion. It is possible that the high osmolality of the tamarisk diet contributed to fixing a maximum allowable intake (Fig. 2). Although mammals are well-equipped to excrete excess sodium with sufficient water consumption, NaCl satiety can result from hyperosmolality and/or dehydration (Stricker and Verbalis 1991).

It is unclear why treatment with PEG in experiment 2 did not promote greater consumption of the tamarisk diet via tannin binding. It is possible that the PEG concentration was not sufficient for the tannin content of the tamarisk diet. Beavers demonstrated the ability to consume significant quantities of tamarisk diet in the absence of PEG treatment despite lacking salivary proteins to bind quebracho tannin (Hagerman and Robbins 1993). Similarly, goats (also incapable of binding quebracho tannins) consumed significant quantities of tannin-containing foods when given experience with the food (Distel and Provenza 1991). In another study, the alteration of exposure to tannin-containing foods with nontannin foods on an every-other-day basis permitted goats to consume greater quantities of tannin diets vs. subjects offered tannin diet exclusively (Kimball and Nolte 2005). Thus, the presence of a tannin-free alternative food in the two-choice tests may have allowed beavers to maximize tannin intake.

In addition to physiological processes for tolerating phytochemicals (e.g., salivary proteins for tannin binding), herbivores can employ a variety of behavioral approaches to manipulate forage palatability. For example, beavers have been observed to soak branches in water, thus leaching phenolics that contribute to poor palatability (Muller-Schwarze et al. 2001). Diet mixing is another method herbivores employ that minimizes consumption of specific plant toxins and antifeedants (Freeland and Janzen 1974). This is a particularly efficient strategy when the various phytochemicals encountered are complimentary (Burritt and Provenza 2000). Toxic phytochemicals are considered complimentary when they act on different physiological systems in the herbivore—allowing the animal to consume greater quantities of the different foods in total than they could of any individual food item. Limiting intake of a

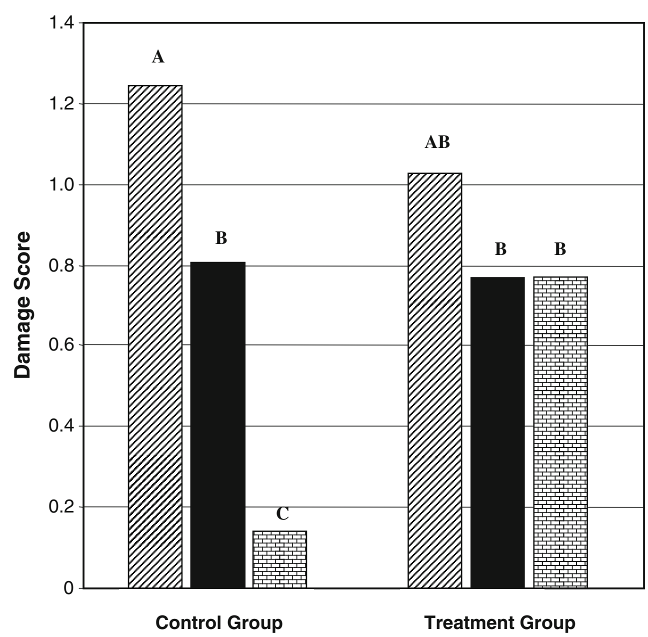

Fig. 3 Species × treatment interaction from the three-way ANOVA of browse scores demonstrates treatment effect on preferences of beavers (N=12) for plant cuttings in cafeteria tests (P=0.001). Casein hydrolysate was applied topically to willow and poplar cuttings in the treatment group. *Different letters* indicate significant differences among damage scores (multiple comparisons) made according to the method of Benjamini and Hochberg 1995) (*diagonally hatched bars S. scouleriana*, *black bars P. nigra*, *crosshatched bars T. ramosissima*)

particular food or phytochemical is not the only regulatory process used by herbivores while foraging. Although few studies have specifically monitored meal patterns, a recent study with ringtail possum demonstrated that intake rate and feeding time are altered in addition to total intake, thus regulating the consumption of deleterious phytochemicals (Wiggins et al. 2006).

Beavers strongly avoided the casein hydrolysate treatment when the control diet was the alternative food (experiment 3; Fig. 1). Avoidance of casein hydrolysate is predictable for most herbivores. Deer (Kimball et al. 2005), mountain beavers, pocket gophers (Figueroa et al. 2008), and guinea pigs (Field, personal communication) have shown strong avoidance responses to casein hydrolysate in single-choice tests. Beavers also avoid plants treated with commercial herbivore deterrents that contain egg or blood products (DuBow 2000).

When tamarisk diet was the alternative food, beavers no longer avoided the casein hydrolysate treatment (experiment 4, Fig. 1). Ironically, protein binding may have contributed to the reduction of casein hydrolysate repellency via diet mixing. Although PEG–tannin binding had no influence on tamarisk diet palatability in experiment 2, tannin–protein binding may have rendered casein hydrolysate more palatable in experiment 4. Self-medicating behavior (in this case, consumption of tannin-containing tamarisk diet that renders the deterrent-treated control diet more palatable) is common among herbivores. In fact, self-regulated PEG intake is the mechanism that makes its use practical in arid rangelands to promote consumption of high-tannin forages (Titus et al. 2000, 2001).

The cafeteria test with plant cuttings (experiment 5) demonstrated that willow was the preferred tree species tested (Fig. 3). In the absence of a deterrent treatment, there was little damage recorded to tamarisk cuttings. Because plant cuttings were not available *ad libitum*, use of tamarisk by the control group was likely influenced by unavailability of the preferred plants as they were exhausted. Deterrent treatment of willow and cottonwood with casein hydrolysate similarly reduced the availability of preferred plants, resulting in a significant increase of tamarisk use (Fig. 3).

Results of this study suggest that deterrent treatment of desirable plant species in wetland areas will facilitate foraging of invasive plants by beavers, including tamarisk. However, maximum intake of tamarisk may be regulated by processes that cannot be circumvented by PEG treatment or supplementation. It is important to emphasize that increased tamarisk consumption by beavers in natural areas holds no promise of tamarisk eradication. Rather, significant use of tamarisk by beavers may decrease the removal of native species and allow natural resources managers to meet management goals in the presence of these efficient ecosystem engineers.

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